Afr. J. mar. Sci. 25: 231–238
2003

OBSERVATIONS ON THE DIEL VERTICAL DISTRIBUTION OF HYDROMEDUSAE IN THE SOUTHERN BENGUELA

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Diel vertical migration (DVM) of six common species of hydromedusae was investigated during two drogue studies conducted in St Helena Bay on the west coast of South Africa in February 1995. *Clytia* spp., *Obelia* spp. and *Bougainvillia macloviana*, were largely confined to surface waters and did not appear to display any DVM. By contrast, *Leuckartiara octona* and *Euphysa aurata* displayed clear DVM and, like *Proboscidactyla menoni,* were found at greater depths than the other species. The depth distribution and amplitude of migration varied between surveys for most species, so definitive interpretations of patterns could not be made.

Key words: Benguela ecosystem, diel vertical migration, hydromedusa

Light, heat, nutrients and oxygen concentrations vary with depth in the oceans, as too do water motion and pressure. These changes result in a layered structure to the ocean, which organisms respond to in either a fixed (McGowan and Walker 1979) or variable manner (e.g. Ambler and Miller 1987). Although variations in vertical distribution may follow a spatial pattern (e.g. latitudinally – Vinogradov 1970), they have been better studied when they follow a temporal pattern (e.g seasonally – Williams and Conway 1981, Buecher and Gibbons 1999; or daily – Roe *et al.* 1984). If there is a degree of spatial return to the pattern, then the variation in the depth of occupancy over a daily cycle is known as diel vertical migration (DVM). The main cue for the behaviour is thought to be light (Verwey 1966), but the causal mechanism is considered to be, among others, predatory avoidance (Gabriel and Thomas 1988). DVM has evolved independently among pelagic taxa, and is seen in all major groups, from photosynthetic micro-algae (Pitcher *et al.* 1998) to fish (Huse *et al.* 1998). The minutiae of DVM (precise depths of occupation, duration of occupancy, etc.) appear to be modified by genetic factors (Gabriel and Thomas 1988), as well as the environment (e.g. Verheye and Field 1992, Gibbons 1993).

Knowledge of the vertical distribution and DVM of plankton off southern Africa is limited, although some data are available for algae (Brown and Field 1985), chaetognaths (Gibbons 1992, Gibbons and Stuart 1994), tunicates (Gibbons 1997), copepods (Peterson *et al.* 1990) and euphausiids (Barange 1990). However, data on the vertical distribution and DVM of hydromedusae are scarce (but see the study by Pagès and Gilli 1992 in the northern Benguela). There is some some evidence to suggest that DVM is displayed by the scyphomedusa *Chrysaora hysoscella* in the northern Benguela (Sparks *et al.* 2001).

Medusae are voracious predators of zooplankton (Matsakis and Conover 1991, Purcell 1992), and there is evidence to implicate them in changes of entire pelagic assemblages (Möller 1984, Purcell *et al.* 1994). Ignorance of the vertical distribution of hydromedusae impacts on the understanding of spatial dynamics of local zooplankton population. This study attempts to redress this lack of knowledge in the southern Benguela.

MATERIAL AND METHODS

Data were collected during two drogue studies conducted in the St Helena Bay region on the west coast of South Africa. The first survey (Survey 1: 17–19 February 1995) was conducted off Cape Columbine (30°10´S, 17°44´E) in water 168 m deep, the second (Survey 2: 20–26 February 1995) in St Helena Bay (32°35´S, 18°07´E) in water 72 m deep.

Zooplankton samples were collected at regular times throughout the day and the night (02:00, 04:00, 10:30 or 12:30, and 20:30) using a 200-µm meshed 1 m^2 multiple opening-closing rectangular midwater trawl (RMT-1×6). The trawl was towed obliquely for a short duration (<1 minute) over five depth strata (Survey 1: ~0–20, 20–40, 40–60, 60–100 and 100–150 m; Survey 2: ~0–10, 10–20, 20–30,

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Manuscript received August 2001; accepted May 2002

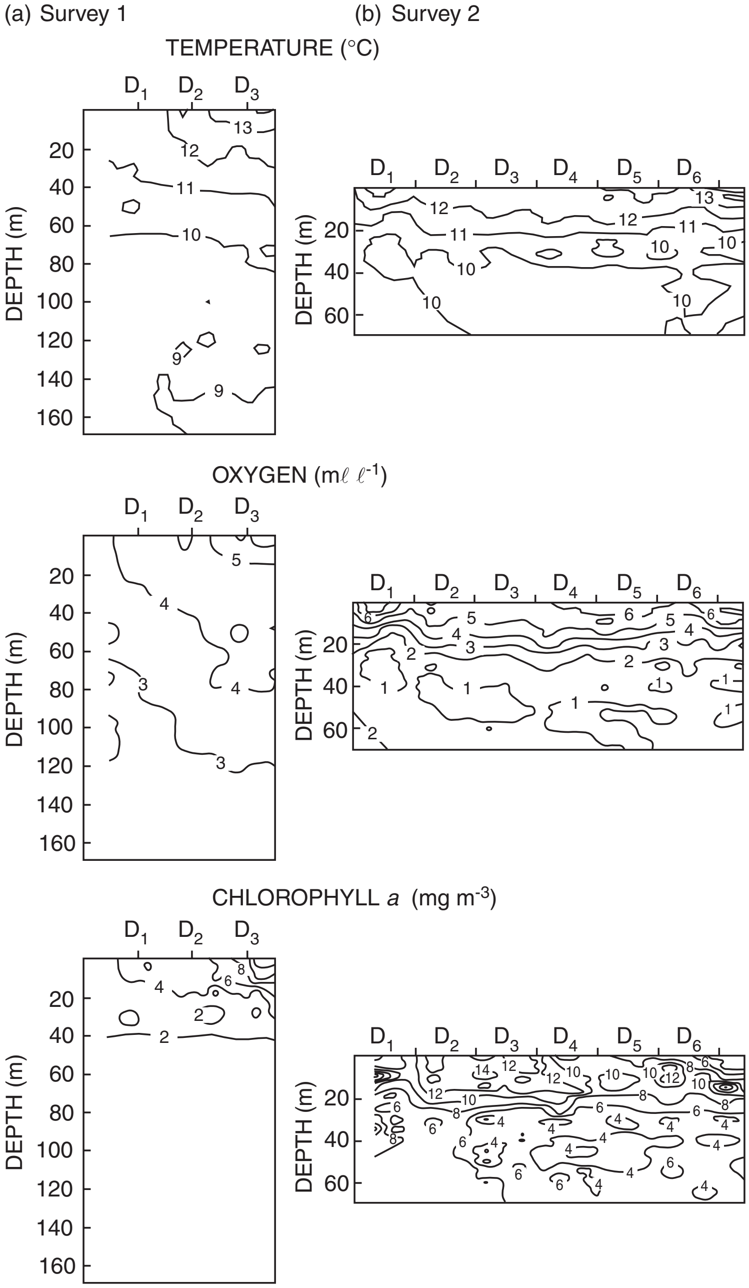

Fig. 1: Temporal variations in the vertical distribution of temperature, oxygen and Chlorophyll *a* concentration during (a) Survey 1 and (b) Survey 2. D_1 denotes first day of sampling (Survey 1; 17 February 1995, Survey 2; 20 February 1995)

Table I: Comparison of day and night total average abundances and weighed mean depth (*WMD*) for the six hydromedusae species collected in Surveys 1 and 2. Average *WDM* was calculated using only the values (depths) where the species were collected. Subscript indices in parenthesis indicate the number of times the species was collected

Species	Survey 1				Survey 2			
	Abundance (Individuals 100 m^{-3} ± *SE*)		*WMD* (m)		Abundances (Individuals 100 m^{-3} ± *SE*)		*WMD* (m)	
	Day n = 3	Night n = 8	Day n = 3	Night n = 8	Day n = 6	Night n = 17	Day n = 6	Night n = 17
E. aurata	$0.4 \pm 0.1_{(3)}$	$0.8 \pm 0.1_{(8)}$	125.3 ± 1.6 <*	74.6 ± 5.4	$0.03 \pm 0.03_{(1)}$	$0.9 \pm 0.03_{(11)}$	2.5 >*	33.5 ± 4.9
L. octona^{+}	$0.3 \pm 0.1_{(3)}$	$0.1 \pm 0.03_{(8)}$	82.7 ± 16.7	61.0 ± 3.6	$0.1 \pm 0.07_{(5)}$ <*	$0.6 \pm 0.1_{(17)}$	15.9 ± 1.9	18.5 ± 2.1
Clytia spp.	nc	$0.003 \pm 0.002_{(2)}$	nc	40.5 ± 4.8	$12.3 \pm 5.0_{(6)}$ >*	$3.6 \pm 1.2_{(15)}$	10.7 ± 1.4	17.8 ± 2.4
P. menoni	$0.01_{(1)}$	$0.003 \pm 0.002_{(2)}$	129.5	101.0 ± 14.7	$0.5 \pm 0.3_{(5)}$	$0.1 \pm 0.03_{(10)}$	20.8 ± 4.5	24.0 ± 4.1
Obelia spp.	nc	nc	nc	nc	$2.0 \pm 0.7_{(5)}$	$1.4 \pm 0.6_{(9)}$	15.3 ± 2.0	15.0 ± 1.0
B. macloviana^{+}	nc	nc	nc	nc	$4.3 \pm 1.5_{(6)}$	$3.4 \pm 1.0_{(17)}$	5.2 ± 0.3	15.2 ± 3.1

nc = Not collected
+ = Presence of ocelli
* Significant differences ($\alpha = 0.05$)

30–40 and 40–60 m). Flow rates were estimated using a flowmeter mounted above the mouth of the net, and 100% efficiency was assumed for each tow. All zooplankton samples were preserved in 4% buffered saline formalin.

Temperature, salinity, dissolved oxygen and chlorophyll concentration were measured (over depth) at regular times (04:00, 09:00, 18:00 and 22:00) throughout the study. The methods used are detailed in Kiørboe *et al*. (1998) and Gibbons *et al*. (1999).

All medusae from the samples were counted, and the stratified density in each depth stratum (indivuals 100 m^{-3}) was calculated from knowledge of the volume filtered by the nets. For every each sampling time, the average abundance (calculated using the abundances in each of the different depth strata) and the weighted mean depths (*WMD*; see Roe *et al.* 1984) of the populations were calculated. The extent of DVM was estimated (when possible) as the maximum distance covered between consecutive day-night estimates of *WMD*. Day and night differences between *WMD* were compared using Student's *t*-test.

RESULTS

During the study period, sunrise was between 06:22 and 06:31 and sunset between 19:27 and 19:38. Detailed descriptions of the hydrological conditions during the surveys are given in Kiørboe *et al*. (1998) and Gibbons *et al*. (1999) and are briefly summarized here.

There was warming of the surface waters during Survey 1 (Fig. 1), causing a deepening of the thermocline (marked by the 10°C isotherm) from 65 (Day 1) to 80 m (Day 2). The water column was isohaline (34.7) throughout. Concentrations of dissolved oxygen and chllorophyll *a* increased in the upper 20 m after Day 1, peaking at 7.21 mℓ ℓ^{-1} and 14.09 mg m^{-3} respectively on Day 3.

In Survey 2, there was an increase in both surface temperature (12 to 14.7°C) and the thermal gradient (3.1 to 5.5°C) over the study period. The temperature was stable (9.4°C) below the thermocline, which was situated between 35 and 40 m. There were diurnal variations in surface temperature, especially at the end of the survey. The water column was isohaline throughout (34.7). The upper layers (>20 m) was well oxygenated (mean 5.8 mℓ ℓ^{-1}), but the oxygen concentration decreased markedly to <1 mℓ ℓ^{-1} below 30 m. Highest chllorophyll *a* concentrations were found in the upper 20 m.

The results given here cover six of the commonest hydromedusae collected. Two species of Anthomedusae (*Euphysa aurata* and *Leuckartiara octona*) and Lepto-

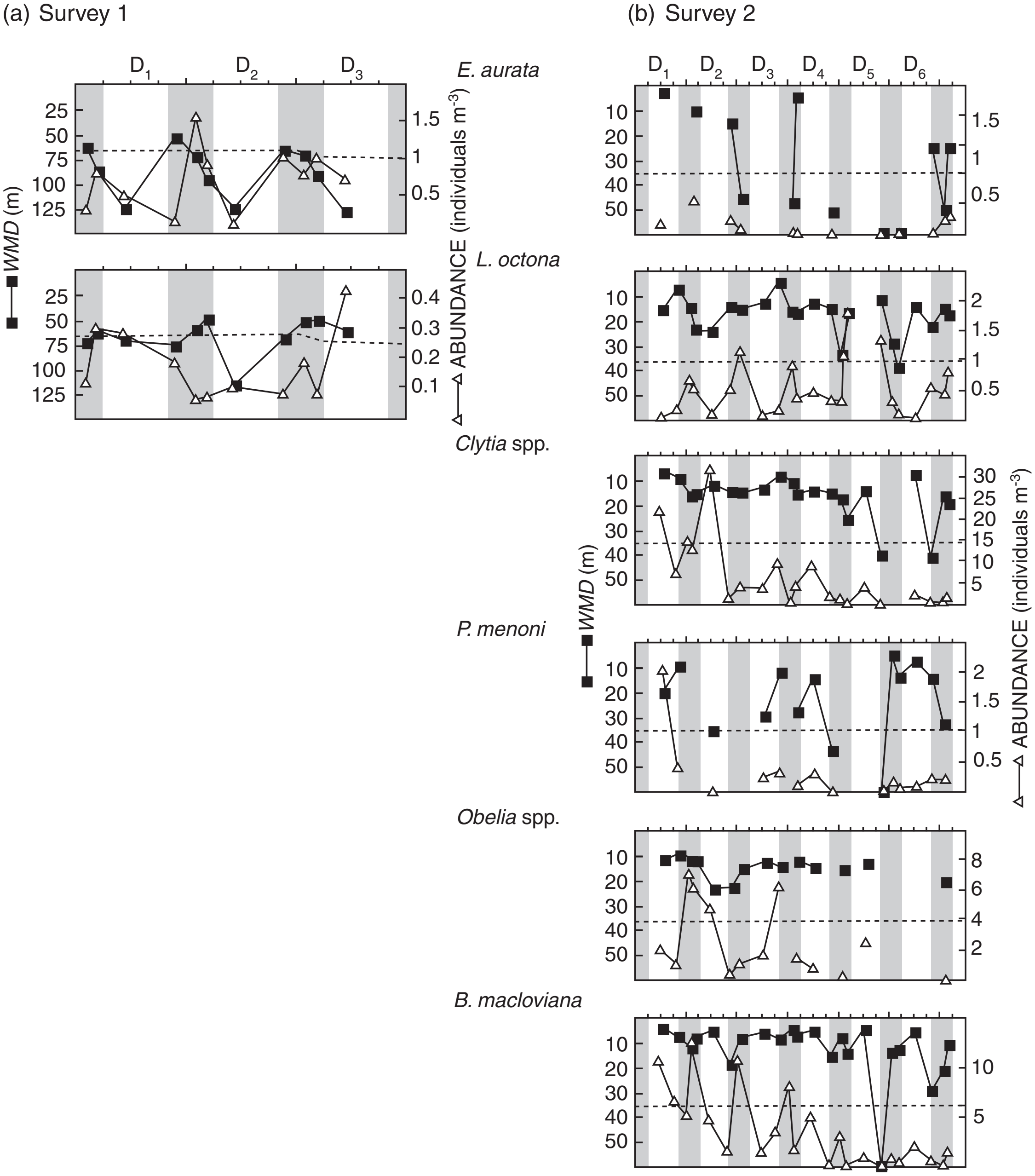

Fig. 2: Temporal changes in the weighted mean depth (*WMD*) and the average abundances of medusae during (a) Survey 1 and (b) Survey 2. The shaded areas are night-time periods and the dotted line indicates the position of the thermocline

medusae (*Clytia* spp. and *Proboscidactyla menoni*) were found in both surveys, and an additional two species, *Bougainvillia macloviania* (Anthomedusae) and *Obelia* spp. (Leptomedusae) were collected during Survey 2. No temporal succession of the different species was noted during either survey. Medusae were most abundant during Survey 2, except for *E. aurata* (Fig. 2).

The most abundant species during Survey 1 was *E. aurata* (Fig. 2), and twice as many individuals were collected at night than during the day (Table I). Maximum abundance averaged 1.6 individuals 100 m^{-3}. *E. aurata* was shallower during the early part of the night than during the day. Its maximum vertical range was 71 m, corresponding to 42% of the water column. *E. aurata* was less abundant on Survey 2 and it was rarely caught during the day, which makes day-night comparisons of either abundance or distribution difficullt. The species was found throughout the water column and appeared to cross the thermocline.

The abundance of *L. octona* varied throughout Survey 1, with no clear diel differences. The species was shallower at night. Because most of the population remained at 60–70 m throughout the survey, the amplitude of migration was difficult to determine. However, it appears that the species can traverse a depth range of 70 m. In contrast, during Survey 2, *L. octona* were more abundant at night than during the day, being restricted to the upper 30 m and above the thermocline.

Clytia spp. was recorded only twice during Survey 1, between 30 and 50 m deep. However, it was the most abundant medusa found during Survey 2, attaining a maximall average abundance of 32.19 individuals 100 m^{-3}. Average abundances differenced significantly ($p < 0.05$) between night and day during Survey 2 and remained in the upper 30 m throughout.

P. menoni were collected three times during Survey 1, between 70 and 130 m deep. During Survey 2, they were collected throughout the water column, but tended to occupy mid-depths. There was no discerniable diel differences in abundance.

The abundcances of *Obelia* spp. and *B. macloviana* during the latter stages of Survey 2. Although there is some evidence to suggest that abundances were highest at night, this was not consistent. The populations of both species were centred in the upper 20 m and DVM was not observed.

DISCUSSION

All the species under study have a global distribution, except in the polar areas (Kramp 1961), and have been collected regularly during previous surveys in the Benguela (Pagès *et al*. 1992, Buecher and Gibbons 2000). Although the overall diversity and the abundance of the medusae were both lower than previously reported in the region (Buecher and Gibbons 2000), this reflects the small number of samples collected, as well as their restricted geographic coverage. For Survey 1, it might also reflect station location, because areas at or close to upwelling regions are believed to have a depauperate (and certainly different) zooplankton assemblage relative to areas downstream (Gibbons and Hutchings 1996). The abundance of medusae (especially meroplanktonic species, as observed here) is extremely variable (Buecher and Gibbons 2000), and refllects current and historic physical processes that result in changes to the autochthanous and allochthanous composition of assemblages.

In the absence of appreciable vertical mixing or advection during the study period (also Gibbons *et al*. 1999), changes in the abundance of medusae linked to the diel cycle (e.g. in the case of *Clytia* spp. or *Euphysa aurata*) can possibly be attributed to recruitment to the water column from deep water, given that the layers above and below the thermocline were moving in slightly different directions (see Gibbons *et al*. 1999). A diel signal to abundance complicates any clear interpretation of DVM, and consequently, discussion is confined here to only those species that showed consistent or unambiguous patterns of verticall distribution.

Three species, *Clytia* spp., *Obelia* spp. and *B. macloviana*, which were common during Survey 2, were largely confined to the upper layers of the water column and did not appear to display any DVM. Such meroplanktonontic species are more common in shallow than in deep water (Moreira 1973) and typically occur above the thermocline. Although several species of *Clytia*, *Obelia* and *Bougainvillia* have on occasions failed to display DVM (Russell 1931, Palma 1985, Ballard and Myers 1996), there are instances when such vertical behaviour has been clear (Russell 1931, Mills 1981). From three different surveys of various duration (1–4 nights) conducted annually between 1924 and 1926, Russell (1931) showed that some species of medusae, especially shallow-water ones, behaved differently from one year to the next. These changes in behaviour are not thought to be intrinsic (Mills 1981) and seem to be controlled mainly by the light intensity (day or moonlight), which also influences the timing of the migrations (e.g. downward migration at night or dawn). If these migrations vary from one year to the next, they can also differ from one season to another (Moreira 1973).

DVM was not clear in *P. menoni* (during either survey), and *L. octona* and *E. aurata* migrated during

Table II: Comparison of vertical migrations from various species of the same genus elsewhere with those observed in the present study. DVM means the population performs an upward migration at night and has a deeper distribution during the day. Reverse DVM means the population has a distribution close to the surface during the day and perform a downward migration at night

Species	Behaviour	Location	Source
Euphysa aurata	DVM	Villefranche Bay, France	Palma (1985)
Leuckartiara octona	DVM	English Channel, UK	Russell (1931)
Clytia simplex	No migration	Benguela current, Namibia	Pagès and Gili (1992)
Phialidium gregarium	Reverse DVM*	Friday Harbor, USA	Mills (1981)
	Reverse DVM	Saanich Inlet, USA	
Phialidium spp.	No migration	Villefranche Bay, France	Palma (1985)
Phialidium spp.	Observation of some upward movement at dusk, but no clear DVM	English Channel, UK	Russell (1931)
Proboscidactyla ornata	DVM	Coast of Santos, Brazil	Moreira (1973)
Obelia spp.	DVM	Coast of Santos, Brazil	Moreira (1973)
Obelia spp.	DVM	English Channel, UK	Gough (1905)
Obelia spp.	No clear DVM	English Channel, UK	Russell (1931)
Bougainvillia spp.	DVM*	Friday Harbor, USA	Mills (1981)
Bougainvillia spp.	DVM	Plymouth, UK	Russell (1928)
B. britannica, B. principis, B. ramosa, B. pyramidata	No migration	Lough Hyne, Ireland	Ballard and Myers (1996)

* Laboratory observations

Survey 1 but not on Survey 2. Species from these three genera have been shown to display DVM (Russell 1931, Moreira 1973, Palma 1985; Table II). However, the species in the present surveys migrated deeper during Surveys 1 and 2 than the depths attained by the species in the aforementioned studies. Russell (1931) observed that macrozooplankton in deep water display clearer patterns of DVM than those in shallow water. Also, Andersen *et al*. (1997) noted that the amplitude of migration of species occupying shallow water was smaller relative to those occupying deeper water. Although *P. menoni* and *L. octona* crossed the thermocline during Survey 2, this boundary limited the vertical migration of the former species in southern Brazil (Moreira 1973).

There was no difference in this study between Antho- or Leptomedusae regarding their DVM or vertical distribution. In contrast, Costello and Colin (1995) suggested that bullet-shaped species (principally Anthomedusae) might be more active than the dish-shaped species, because of their better jet propulsion. Also, there was no relationship between DVM and the presence of light-sensitive ocelli in the species under study (Table I). Although ocelli have been shown to play a role in DVM of some medusae species (Mills 1983), other studies have found that ocelllli were not always present in light-sensitive migrating species (Moreira 1973, Mills and Goy 1988). However, some photosensitive neurons have been recognized as responsible for a swimming reaction when stimulated by light (Anderson and Mackie 1977), which can then initiate migratory behaviour.

Despite the present inconclusive results (largely on account of low animal densities), to the authors' knowledge the present data represent the longest published time-series describing DVM of Hydromedusae. The discrepancies and inconsistencies in the patterns found here over three and six-day surveys emphasize the fact that 24 h of observations are not adequate to describe the migrating behaviour of medusae definitively. The fact that the present observations are contradictory and sometimes contrast with previous observations show the lack of understanding about DVM of the species under study. For example, Mills (1981) suggested that DVM of medusae allows individuals to concentrate close to the surface for reproductive purposes. However, such factors as presence of prey, pressure changes within the water column or diel differences in buoyancy need to be taken into consideration to explain vertical distribution of medusae (Arai 1992). Further observations are clearly necessary to understand this migratingory behaviour and the biotic and abiotic factors that control it.

ACKNOWLEDGEMENTS

We thank the officers and crew of the F. R. S. *Africana* and our colleagues for their co-operation and assistance at sea. The National Research Foundation is gratefully acknowledged for financial support.

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